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Studies on the Enchytraeidae (Oligochaeta) of Moorland Soil

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With 4 figures in the text

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Contents

1 Introduction

Widespread interest in the family Enchytraeidae was not established until the development of soil extraction techniques by NIELSEN (1952) and O'CONNOR (1955). These techniques have made possible quantitative surveys, which in turn have stimulated a critical revision of the taxonomy (NIELSEN & CHRISTENSEN 1959). The present paper describes sampling surveys carried out on the Moor House National Nature Reserve, Westmorland, England (Grid reference NY 75,32), from 1956 to 1958, to establish the relative reliability and limits of error of sampling and extraction methods and to evaluate some of the main aspects of enchytraeid distribution.

2 Study Area and Climate

The study area described by CRAGG (1961), was situated on the eastern part of the Reserve, which forms the N. E. dip slope of the Yordale series of Carboniferous sandstones, shales and limestones, in general covered with blanket bog, in various stages of erosion and recolonisation. Numerous streams run through the area to join the River Tees. Five sample sites were chosen as described in table 1.

Table 2 shows rainfall, precipitation/evaporation ratios (P/E) and air temperatures at Moor House compared with lowland stations. The climate at Moor House is much cooler and P/E higher — about three times as much water is gained from the atmosphere by the soil than at lowland stations.

Relevant to the period of study, the following notable climatic conditions were experienced:
1955 — unusually hot and dry summer, with P/E ratio less than unity, followed by a mild early winter.
1956 — a cool and very wet August and mild winter.
1957 — a dry June with P/E ratio less than unity.

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Table 1. Description of sample sites.

Sample site	Bare peat	*Juncus* 56	*Juncus* 57	*Nardus* grassland	Alluvial grassland
Grid ref.	758317	756325	765329	757319	757329
Altitude (m. O. D.)	633	564	556	602	549
Situation and drainage ..	flat, very exposed	E-facing, sheltered gentle slope, receiving site	S-facing, sheltered gentle slope, receiving site	E-facing exposed slope	flat, sheltered
Soil description	waterlogged peat	waterlogged peat on freely-drained mineral soil	waterlogged peat on very poorly drained mineral soil	imperfectly drained mineral soil	freely-drained mineral soil
% soil organic carbon (dry wt.)[1]	38	30	30	16	7
C/N ratio[1])	34	15	15	18	8
Vegetation	none				
dominant..............		*Juncus squarrosus* L.	*Juncus squarrosus* L.	*Nardus stricta* L.	*Festuca ovina* L.
abundant..............		*Polytrichum commune* L. *Deschampsia flexuosa* L.	*Deschampsia flexuosa* L. *Festuca ovina* L.	*Galium hercynicum* WEIGEL	*Thymus serpyllum* L.
Soil horizons (cm.)					
dry loose litter (A_0L)[2]) ..	—	0—2	0—2	0—4	—
moist active litter(A_0L+F)	—	2—4	2—4	4—6	—
humified layer (A_0H) ...	0—240	4—80	4—42	6—40	—
soil (A_1)		80—	—	—	0—26
(A_2/G_3)			42—67	—	
(B_2)				40—53	

1) Data from CRAGG (1961).
2) Discarded when taking soil cores.

Table 2. Annual climatic factors for Moor House and two lowland stations.

Station	Altitude (m.)	Rainfall (cm.)	P/E ratio	Air temp. (° C.)
Moor House	561	178	4.0	5.6
London	8	58	—	10.6
Doncaster	8	64	1.3	—

3 Sampling and Extraction Techniques

As indicated in table 1 dry loose surface material was discarded as inactive when soil sampling. On each sampling occasion during 1956—1957, fifteen pairs of soil cores were taken randomly from the sample area of 100 sq. m.; each soil core being 6 cm. deep and 7.3 cm. in diameter. One of each pair of soil cores was extracted by the NIELSEN (1952) method and the other core by the wet funnel method (O'CONNOR 1955). These comparisons (PEACHEY 1962) showed that variations in relative efficiency were related to soil type, age, species composition and vertical distribution of the worms. The wet-funnel method proved to be more reliable than the NIELSEN method and more convenient for peaty soils.

Using a smaller core-size of 3.5 cm. diameter the wet-funnel method was used in 1957—1958 for soil cores taken from the *Juncus* 57 site which was divided into five sub-plots to permit the statistical analysis of sample data for variation in the site and in the extraction method. On

9 sampling occasions from May—November, 1957, 9 soil cores were taken from each of the five sub-plots, making 45 soil cores in all. Additional census data was obtained from 15 soil cores only.

Sampling for microdistribution studies was based on the complete extraction of adjacent soil blocks within the specified area.

Weights of live worms were obtained as described by NIELSEN (1955a).

4 Analysis of Sampling and Extraction Data

The sample data obtained from the *Juncus* 57 site were statistically analysed (Table 3) for sampling and extraction errors compared to seasonal variation: the latter was shown to be the only significant factor ($F = 59.73$, $P < 0.001$).

Table 3. Analysis of variance of *Juncus* 57 data.

Component of variance	Degrees of freedom	Sum of squares	Mean square	Variance ratio (F)
1. Seasonal	8	1,609,385	201,173	59.73[1])
2. Sub-plots (overall)	4	16,118	4,030	1.20
3. Extractions (overall)	1	20	20	0
4. Funnel rows (overall)	1	101	101	0
5. Funnel pairs (overall)	14	28,089	2,006	0.60
6. Sub plots (2) + seasonal (1)	32	95,408	2,982	0.89
7. Extractions (3) + seasonal (1)	8	27,610	3,451	1.05
Error	336	1,131,658	3,368	—
Total	404	2,908,389	—	—

1) $P < 0.001$

The seasonal factor was then eliminated in a series of separate analyses for each sampling occasion but only one out of twelve gave a significant ($P < 0.01$) variance ratio for the variation in replicated mean estimates.

5 Distribution

5.1 Qualitative distribution

The present study was completed before the taxonomy proposed by NIELSEN & CHRISTENSEN (1959) had been published and only broad generic groupings were indicated (Table 4).

The generic composition differed from that found by NIELSEN (1955a) in lowland sites where *Fridericia* is often dominant. *M. sanguineus* is a new species erected by NIELSEN & CHRISTENSEN for specimens described from Moor House and from a flush bog in W. Jutland. Its distribution at Moor House is sharply restricted to habitats on shallow peat at the moor

Table 4. Generic list and composition within sample areas on the Moor House reserve.

Genus	Approx. % of total enchytraeid density	Sample area
Cognettia / *Cernosvitoviella* / *Marionina*	100	Bare peat
	98	*Nardus* grassland
	90	*Juncus* 56 & 57
	75	Alluvial grassland
Mesenchytraeus		
e. g. *M. sanguineus* n. sp.	10	*Juncus* 56 & 57
	occasionally	*Nardus* grassland
e. g. *M. flavus* LEVINSEN	2	*Nardus* grassland
Fridericia		
e. g. *F. magna* FRIEND	25	Alluvial grassland

edge, with *J. squarrosus* as the dominant vegetation. *M. flavus* is occasionally found in *Nardus* grassland and in *J. squarrosus* areas in dryer conditions than *M. sanguineus* as well as in moss carpets on waterfalls. In Denmark it is characteristic of damp places. *Fridericia magna* the largest species at Moor House is endemic to Britain. It is found in the grassland on alluvium and in sheep droppings on these and similar areas.

5.2 Microdistribution

5.21 *Non-normal distribution*

PEACHEY (1962) describes the positive skew and excess of small negative deviates characteristic of the sampling distributions obtained from the Moor House sites and similar to those found by NIELSEN (1954) and O'CONNOR (1957). Using random sample data a more sensitive test was applied, in April, 1957 to 75 sample unit values obtained from the *Juncus* 57 site, by using statistics for skew (g_1) and kurtosis (g_2) as described by SNEDECOR (1956). The values obtained and their significance levels are given in table 5.

Table 5. Values of the statistics for skew and kurtosis in *Juncus* 57 data.

Data	skewness (g_1)	kurtosis (g_2)
Untransformed	+ 0.564[1])	— 25.24[2])
Log. transformed	— 0.005	+ 3.20[2])

1) $P < 0.05$
2) $P < 0.001$

The positive value of g_1 indicates an excess of below-mean values in the sampling distribution and the negative value for g_2 shows an excess of near-mean values. The effect of logarithmic transformation was to eliminate skew and to reduce kurtosis.

5.22 *Non-random distribution*

The mean and standard deviation were related in a similar way to that found by NIELSEN and O'CONNOR. Table 6 shows that as the mean increases in value, so does the standard deviation, but the latter does not increase so much at the higher mean values. The coefficients of dispersion or ratio of variance to means (SALT & HOLLICK 1946) were well above unity, indicating an aggregated distribution.

Table 6. Relationship of mean values to variance statistics for the *Juncus* 57 data.

Mean value	Standard deviation	% standard deviation	Coefficient of dispersion
50	25	50	13
100	40	40	16
150	50	33	17
200	60	30	18
250	70	28	20

5.23 *Complete enumeration of microdistribution*

A direct idea of soil microdistribution of enchytraeids was obtained by complete enumeration of a portion of the bare peat site, in May, 1957 by the extraction of 100 square blocks, each 10 sq. cm. in area and 6 cm. deep. The soil blocks were randomised for extraction in three lots, by the wet-funnel method. The individual soil block densities so obtained were mapped (Fig. 1a) and gradients revealed by using standard deviation intervals as contours.

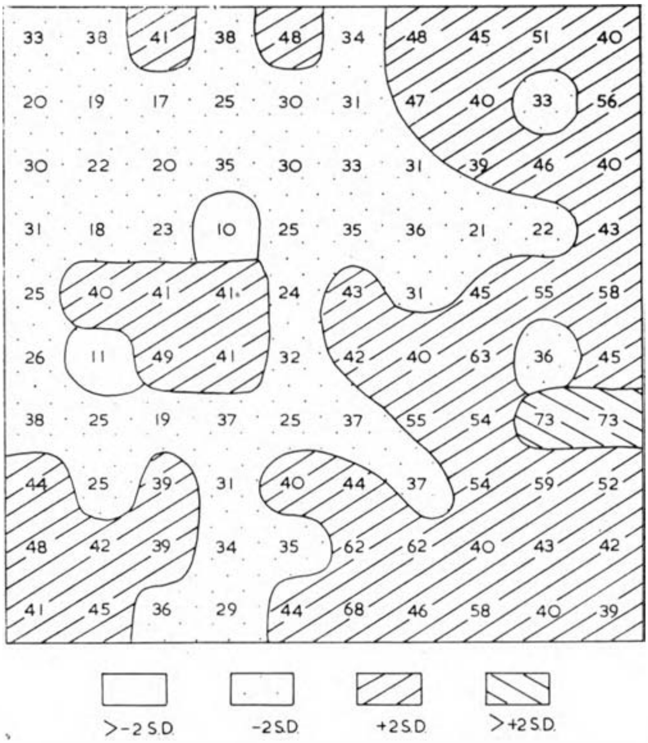

Fig. 1a. Density map of bare peat obtained by complete enumeration.

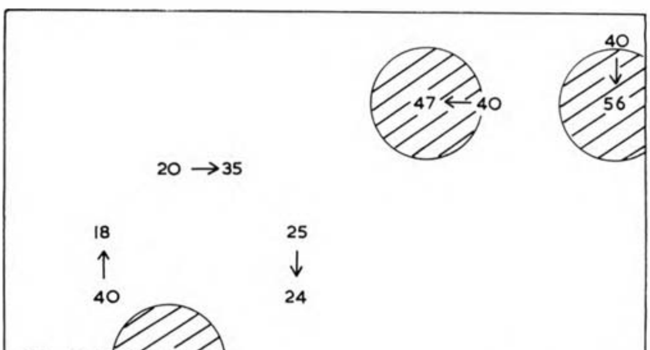

Fig. 1b. Density map of bare peat obtained by tie-line sampling.

The mapping shows the break-up of high-density patches within more continuously distributed lower densities. The analysis of variance (Table 7) revealed that the extraction factor was insignificant compared to the significant gradients ($P < 0.001$) within the plot.

Table 7. Analysis of variance of the microdistribution plot.

Component of variance	Degrees of freedom	Sum of squares	Mean square	Variance ratio
Rows along	9	3,563	396	4.3*)
Rows down	9	4,855	539	5.8*)
Extractions	3	371	124	1.3
Error	78	7,259	93	
Total	99	16,048	162	

*) $P < 0.001$

The coefficient of dispersion for the plot, 4.2, exceeded the limits of the coefficient for random distribution which are 1 ± 0.2858.

SALT and HOLLICK used the analysis of variance to remove from the total variance of the plot a component for grouping of adjacent soil block values and then compared the coefficient of dispersion values for total variance and remainder variance. They argue that if the coefficient of dispersion for the remainder variance is less than that of the total variance, then the aggregations are contained disproportionately within the larger grouping. Table 8 illustrates the effect of varying the size of the grouping on the remainder coefficient.

Table 8. The remainder coefficients of dispersion after the removal of components for larger groupings.

Component removed		
Area of grouping (sq. cm.)	Number of soil blocks in grouping	Coefficient of dispersion
10	no removal	4.2
40	4	2.1
250	25	2.6
500	50	3.1

The remainder coefficient (obtained after the component, for groups of 4 adjacent soil blocks, had been removed) was equal to half the value of the total coefficient, but other remainder coefficients, calculated after the removal of components for larger groupings were not so reduced. From this it is concluded that the main aggregation effect was contained within the area (40 sq. cm.) occupied by four adjacent soil blocks.

5.24 *Tie-line sampling*

The labour involved and the destruction of the test plot are disadvantages of the complete enumeration method. The effect of tie-line sampling, as described by HUGHES (1962) was tried by taking, at random, ten soil block values from fig. 1a and adjacent to each of these, but in a direction, changing by 90° a second value was taken (fig. 1b). These ten pairs of sample units were said to be connected by a tie-line (q) of length 3.16 cm. from the centre of one block to the centre of its pair. The sample units were divided into frequency classes (Column I in table 9) and the frequency (F in column II) accumulated (F_a in column III). From this the probability of a random sample falling within an aggregate (P_a in column IV) is calculated from $P_a = 1 - (F_a/20)$. Column V shows the tie-lines and the number of tie-lines that cross the class boundaries. The probability that the tie-lines will cross the edge of the aggregate (P^c in column VI) is calculated directly from the number

of tie-line crosses. The mean radius (r in column VII) is obtained from the expression $r = 4qP_a/\pi P_c$, because theoretically $P_a = \pi r^2/A$ and $P_c = 4\,rq/A$, where A = the area of the test plot. The mean number of aggregates (n in column VIII) is calculated from $n = P_c^2\,A\pi/16\,q^2P_a$. The last two columns show the smaller size and larger number of aggregates at above-mean (+ 40) density levels.

Table 9. Aggregate system in the bare peat plot as determined by the tie-line sampling method.

(I) Frequency class	(II) F	(III) F_a	(IV) P_a	Tie-line	(V) Tie-line crosses	(VI) P_c	(VII) Mean radius (r)	(VIII) No. of aggregates (n)
65+	2	20	0		0	0	—	—
65—	2	18	0.10		2	0.2	2.0	8
60—	1	16	0.20		3	0.3	2.7	9
55—	0	15	0.25		3	0.3	3.3	7
50—	3	15	0.25		4	0.4	2.5	13
45—	0	12	0.40		4	0.4	4.0	8
40—	3	12	0.40		3	0.3	5.3	4—5
35—	2	9	0.55		3	0.3	7.3	3
30—	1	7	0.65		4	0.4	6.5	5
25—	2	6	0.70		4	0.4	7.0	4—5
20—	3	4	0.80		1	0.1	—	—
15—	1	—	0.95					

This is emphasised in Table 10 where the above-mean estimates have been grouped for comparison to the below-mean estimates. From this tie-line sampling it can also be concluded that the distribution breaks up into discontinuous patches at higher densities. These have been graphically represented in Fig. 1 b.

Table 10. Aggregate estimates of Table 9 grouped into above mean and below mean values.

Density	(VII) Average mean radius cm.	(VIII) Average number of aggregates
40+ above-mean values	2.9	9
40— below-mean values	6.5	4

5.3 Vertical distribution

5.31 *Surface samples*

Table 11 shows that in 1957 most of the worms extracted from 0—6 cm. soil cores taken from *Juncus* and *Nardus* sites were concentrated in the $A_0L + F$ layer. In the bare peat

Table 11. Overall % numbers of worms in the top layer of 0—6 cm. samples, 1956—1957.

Sample site	Top layer 0—2 cm.	% in top layer overall	under 5 °C.	over 10 °C.
All species				
Juncus 56	$A_0L + F$	63	50	78
Nardus	$A_0L + F$	77	66	88
Bare peat	A_0H	43	30	67
Alluvial grassland	A_1	59	39	76
Mesenchytraeus				
Juncus 56	$A_0L + F$	21	7	35
Fridericia				
Alluvial grassland	A_1	29	—	—

and alluvial grassland, with no litter layer, worms were less superficially distributed, as were *Mesenchytraeus* and *Fridericia* considered separately. Worms in all sites were sensitive to soil temperature and moved upwards in warm weather.

For *Nardus* grassland, soil temperatures and percentages of worms in the $A_0L + F$ layer were correlated ($r = 0.841$, $P < 0.01$) and for *Mesenchytraeus* in the *Juncus* site, $r = 0.687$, ($P < 0.02$).

5.32 *Depth samples*

Deeper sampling in the autumn of 1955 showed that over 75% of the worms were in the top 6 cm. of 12 cm. deep samples. Depth sampling in the *Juncus* 56 site in January and May, 1956 revealed a similar zonation but with a slightly deeper distribution in the colder month, more pronounced when *Mesenchytraeus* was considered separately (Table 12). On each of the sampling occasions, P/E ratios were above unity.

Table 12. % vertical distribution of enchytraeids in the *Juncus* 56 site, 1956.

Month	Max.-min. monthly temp. (°C.)	Depth of soil core 0—6 cm.	6—11 cm.	11—16 cm.
(All species)				
Jan.	0	81	13	6
May	7	90	9	1
(*Mesenchytraeus*)				
Jan.	0	31	43	26
May	7	94	5	1

On eleven selected sampling dates throughout 1957—1958 depth samples were taken in the *Juncus* 57 site. On all but three of the sampling dates (Table 13) over 90% of the enchytraeids and *Mesenchytraeus* considered separately were found in the top 6 cm. and on all these occasions the P/E ratio for the previous 14 days was greater than unity. On the remaining occasions, the P/E values were below unity and over half the enchytraeids had moved downwards, below the top 6 cm. The P/E values were correlated after suitable transformation with the percentage in the 0—6 cm. layer ($r = 0.831$, $P < 0.01$).

Under drying conditions on 9th July, 1961 a soil sample was taken down to 30 cm. and 20% of the worms were extracted from below 12 cm. depth.

5.33 *Weight and vertical distribution*

It was observed that young worms were missing from deeper samples and this was confirmed by weighings carried out in July, 1957. Table 14 gives significant differences ($P < 0.01$) in mean weight of worms extracted from different depths.

5.4 Seasonal distribution

5.41 *Census data* 1956—1957

The 0—6 cm. sampling data for 1956—1957 showed significant fluctuation in the density of enchytraeids in all sites (Fig. 2). Peak densities were recorded in the wet late summer or in the autumn except for *Nardus* grassland in which densities increased throughout the sampling period. In July and August, during the period of rapid increase in numbers, P/E = 4, compared to the previous five months when P/E = 2. There was, however, no drought during the period and an April—May drop in numbers in the *Juncus* 56 site does not appear to be related to any climatological factor.

Table 13. Vertical distribution (census data in %) of enchytraeids in the *Juncus* 57 site and P/E ratios for the fortnight prior to sampling.

Date	0—6 cm. All species	6—12 cm. All species	0—6 cm. *Mesenchytraeus*	6—12 cm. *Mesenchytraeus*	P/E for previous 14 days	
25/6	34	66	80	20	0.008	dry
2/7	40	60	70	30	0.443	dry
9/7	48	62	60	40	0.995	dry
25/7	98	2	100	0	2.5	wet
19/8	99	1	100	0	11.5	wet
25/9	100	0	100	0	3.1	wet
22/10	98	2	100	0	3.3	wet
22/11	96	4	100	0	4.7	wet
9/12	100	0	100	0	2.7	wet
28/12	90	10	91	9	frozen	wet
30/4	100	0	100	0	> 2.0	wet

Table 14. Differences in mean weight per worm (*Mesenchytraeus* excluded) extracted from two sample depths.

Depth of sample (cm.)	Mean weight per worm (mg.)
0— 6 cm.	0.174 ± 0.029
6—18 cm.	0.224 ± 0.004

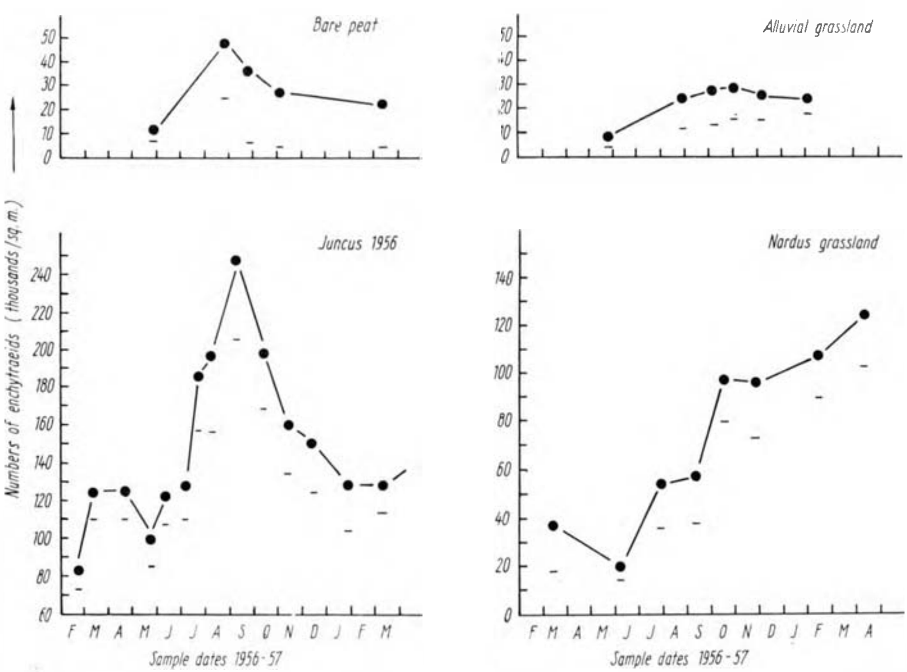

Fig. 2. Density fluctuations of enchytraeids in four sample sites 1956—1957 (with — 2 S.E. limits).

5.42 *Census data* 1957—1958

Detailed sampling on the *Juncus* 57 area gave a correlation between 0—6 cm. sample numbers and P/E ratios ($r = 0.602$, $P < 0.01$) obtained throughout 1957—1958. Part of this correlation was due to downward movement of the worms at P/E ratios below unity (Table 13). Using data from depth samples where necessary, monthly average estimates for the complete distribution were compiled (Fig. 3); they show a similar fluctuation to that found in the previous year in the *Juncus* site. Density increase was related to rising P/E values though *Mesenchytraeus* considered separately, did not give such a clear trend. Later sampling showed that the April—May drop from 240,000 to 180,000 per. sq. m. in 1957 was repeated in 1958 when a decrease from 250,000 to 180,000 per sq. m. was recorded. As with the *Juncus* 56 results, these April—May decreases were not related to climate nor to downward movement.

Significant decreases in mean weight of worms extracted were found during periods of density increase (Fig. 4) in the *Juncus* 56 ($P < 0.001$) and *Juncus* 57 ($P < 0.01$) sites and for *Mesenchytraeus* considered separately, ($P < 0.001$) in 1956.

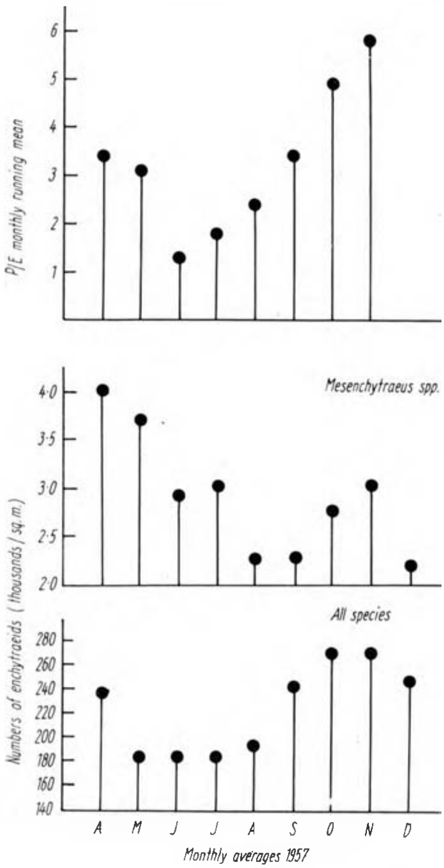

Fig. 3. Monthly fluctuations of enchytraeids in the *Juncus* 57 site with precipitation/evaporation ratios for 1957.

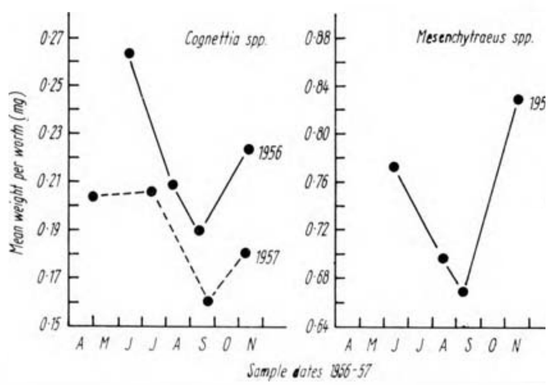

Fig. 4. Seasonal fluctuations in mean weight of worms extracted from *Juncus* 57 samples.

5.43 *Annual estimates* 1956—1958

Spring estimates, were compared over three years (Table 15) for *Juncus* and the *Nardus* sites and although the former remained fairly constant, the *Nardus* densities increased each year. This increase can be related to P/E values for the preceding August of each year, i. e., a low density was recorded after the dry summer of 1955, but increases followed the wet August of 1956 and 1957.

5.5 General distribution and abundance

Both the numbers and biomass of enchytraeids were the highest in the *Juncus* sites, high in the *Nardus* grassland and low in bare peat and alluvial sites (Table 16).

Table 15. Spring estimates for 1956, 1957 & 1958 and computed P/E values for the preceding Augusts.

Site	thousands/sq. m. *Juncus* 56	*Juncus* 57	*Nardus*	P/E for preceding August
1956	126 ± 15	—	37 ± 19	0.7
1957	147 ± 32	227 ± 30	124 ± 21	6.6
1958	155 ± 19	257 ± 58	204 ± 36	4.3

Table 16. Peak densities and live biomass estimates for the enchytraeids in the five sample sites.

Date	Sampling sites	Density thousands per sq. m.	Biomass g./sq. m. live wt.
11/57	*Juncus* 57	289	53 (2)
9/56	*Juncus* 56	248	51 (6)
4/58	*Nardus*	204	35[1])
8/56	Alluvial	25	15 (10)
8/56	Bare peat	49	10

1) Estimated biomass interpolated from last weight measurement in autumn, 1956.

Figures in brackets refer to *Mesenchytraeus* included in *Juncus* samples and *Fridericia* included in alluvial grassland samples.

Table 17 shows that the higher densities of enchytraeids, gave lower mean weight per individual, after the exclusion of *Mesenchytraeus* and *Fridericia*.

Table 17. Mean weights for peak densities in the five sample sites (*Mesenchytraeus* and *Fridericia* excluded).

Date	Sampling sites	Mean wt. per worm (mg.)	Density (thousands/sq. m.)
11/57	*Juncus* 57	0.160	261
9/56	*Juncus* 56	0.189	239
11/56	*Nardus*	0.180	96
8/56	Bare peat	0.211	49
8/56	Alluvial	0.225	24

6 Discussion

6.1 Techniques

The adoption of a formal sampling design in 1957–1958 for *Juncus* 57 samples made possible the analysis of the data obtained for errors or bias in the sampling or extraction procedure and confirmed the validity of the density estimates and the consistency of the wet-funnel extractions (Table 3).

6.2 Microdistribution

The g_1 and g_2 statistics confirmed the positive skew and negative kurtosis, non-normal characteristics of enchytraeid sampling distributions. The usefulness of logarithmic transformation on distributions of this kind was emphasised by the reduction in skew and kurtosis, when the g statistics were applied to transformed data (Table 5). The distributions were also aggregated as shown by the high value of the coefficients of dispersion (Table 6).

A direct picture of microdistribution was obtained by the complete enumeration method. This showed the excess of near-mean values, distributed as a matrix in which the isolated patches of higher density occurred (Fig. 1a). The tie-line sampling gave a similar, but less accurate picture (Table 9) indicating a break-up of the distribution at above-mean densities.

Both methods indicated that the high density patches occupied an area of about four soil cores, equal to a radius of about 3 cm. (Tables 8 & 10). Estimates of aggregation size and number were naturally subject to a large error, when estimated by tie-line sampling. However, a normal census programme could be easily adapted to tie-line sampling and may consequently reveal trends in population microstructure at differing density levels.

The aggregation of worms may be caused by the slow rate of dispersion from a rapidly increasing reproductive centre, However, the heterogeneity in the sample area must also be considered and there is no reason why soil animals should be randomly distributed under such conditions. NEYMAN and SCOTT (1957) have described the mathematical theory which permits considerations of the population as a collection of clusters. SKELLAM, in the discussion on this paper mentions the tendency to leptokurtosis, perhaps due to variations between organisms in their powers of dispersion. In the absence of detailed knowledge of enchytraeid physiology and ecological requirements, aggregation studies must remain speculative and their chief value lies in helping to design and assess the significance of sampling programmes.

6.3 Vertical distribution

The enchytraeids were concentrated in the ($A_0L + F$) layer where present (Tables 11, 12 and 13). Downward movement followed cold or drying conditions. The older and larger worms appeared to be capable of moving deeper than young worms (Table 14). The superficial zonation at Moor House is probably emphasised by the almost continual moist condition of the surface layers of the soil.

IVLEVA (1953) has shown that *Enchytraeus albidus* will actively move from dry to wet soil. provided that desiccation is not imminent. NIELSEN (1955b) and O'CONNOR (1957) did not find such a downward movement, NIELSEN puts this down to the absence of a clear moisture gradient in the very sandy Jutland soils and O'CONNOR ascribes changes in vertical distribution to differential mortality. The moisture gradients in the Moor House wet peat sites, when downward movement occurred from the drying surface, were very clearly defined, assisted by the impeded drainage and moisture retaining capacity of the peat below the surface layers. The mineral soils would not have provided such clear gradients and the density increase in the *Nardus* grassland (Table 15) suggests that in this site a refuge from drought in the summer of 1955 was not available to the worms, or that they were not able to reach moister layers.

IVLEVA also showed that *E. albidus* moves away from waterlogged conditions to a moisture content optimum of 21 %. This response appears to be associated with respiratory needs and may account for the rapid return at Moor House to a superficial distribution, with the advent of wetter conditions.

Although there was an upward movement under warm conditions (Table 11), the soil temperature at Moor House never exceeded 12 °C. on any of the sampling occasions. IVLEVA found that *E. albidus*, a lowland species, preferred a temperature of about 17 °C. It is not thought that soil temperature during the present study was ever a direct limiting factor on distribution, though NIELSEN (1955b) has pointed out that in nature, soil temperature and moisture cannot be separated. The main reason for deep vertical fluctuations in distribution at Moor House was the desiccation threat. The absence of a cuticle and a high surface area/volume ratio makes these soil animals very vulnerable to drying out.

6.4 Seasonal distribution and general abundance

Seasonal distributions were in general characterised by a late summer or autumn peak density occurring under wetter conditions and followed in all sites by a winter return to pre-peak values except in the *Nardus* sites. There was also a spring fall in density in the

Juncus sites in each of the three sample years. Weight measurement showed that the increase in density in later summer was due to the addition of young worms to the distribution (Fig. 4) especially in *Juncus* and *Nardus* samples (Table 17). There was an absence of mature *Cognettia* in all the samples, even though this was a common genus. CHRISTENSEN (1959) has described the reproduction of *C. sphagnetorum* in terms of an asexual fragmentation process.

It has already been argued that the annual density estimates (Table 15) obtained in the spring of the 3 consecutive years following the dry summer of 1955, reflect the relative vulnerability of worms in the *Nardus* site to desiccation compared with the peat sites which have moist deeper layers even under drying conditions (Table 13).

The biomass of enchytraeids was highest for the *Juncus* sites where the desiccation threat was the least and where there was a well developed $A_0L + F$ layer (Table 16). In the bare peat site, the absence of vegetation may have had a direct effect on the density in terms of food limitations, as this site has the highest C/N ratio. The lower biomass of the *Nardus* site probably reflected the effect of drought in 1955. The peak densities recorded by JEGEN (1920) and NIELSEN (1954. 1955a) were preceded by summer minima during unfavourably dry spells. In some areas in 1954, NIELSEN found that nearly all the worms had been killed off, within a fortnight of the beginning of drought. There were no significant summer minima at Moor House during the period 1956—1958, which apart from the dry early summer of 1957 was wet, with P/E values generally well above unity. O'CONNOR did not find summer minima and attributes this to the absence of summer droughts, except in 1955.This unusually hot and dry summer was also experienced at Moor House and it has been inferred that worms in the mineral soil-type areas at Moor House suffered from drought subsequent recovery taking at least two years. The stability of densities in the *Juncus* sites from year to year following 1955 and the evidence of downward movement during surface drying indicates a greater freedom from drought, as a limiting factor.

In ecological thinking about density limitation there is controversy between the climatic school, postulating density independent control (DAVIDSON and ANDREWARTHA 1948a & b) and the competition school which maintains the importance of density dependent factors (NICHOLSON 1957). Using data on the fluctuations in field populations of *Enchytraeus albidus* in Huddersfield sewage beds, REYNOLDSON (1957) has suggested that the importance of density dependent control varies with the general physical favourability of the environment. This approach may help in the present study. In the *Juncus* sites, physical favourability can be considered to be high, as the worms are well protected from desiccation. Compared with these sites, the *Nardus* grassland is physically less favourable. In the winter of each of the sample years, the *Juncus* densities have returned to pre-peak values but there is no evidence of a climatic factor, because at the same time *Nardus* densities were increasing. In this case it is suggested that the return to pre-peak values in the winter and the April to May drop in the *Juncus* site may be caused by an unknown density dependent factor. BIRCH (1957) has put forward the view that the laws which govern the abundance of animals also govern their distribution. When overall density and biomass estimates are considered, the distribution as well as the abundance of Moor House enchytraeids appears to be linked with the physical favourability of the site. The *Nardus* and alluvial grassland can dry out, the bare peat is subject to violent changes in temperature and moisture and only the *Juncus squarrosus* moor provides an almost permanently moist $A_0L + F$ layer in which the highest densities and biomass of field populations of enchytraeids have been found. In addition this habitat has a much lower C/N ratio than the other peat site (Table 1).

CRAGG (1961) collected together the information on numbers and biomass of the Moor House soil fauna. In spite of obvious errors in determining live weight estimates, the present study has emphasised the importance of enchytraeids in the Moor House ecology, particularly in the *Juncus squarrosus* moor and other peaty sites where as small individuals, they

amount to a substantial biomass. This contrasts with the alluvial grassland where earthworms are more abundant (SVENDSEN 1957) and where the smaller enchytraeid biomass is made up of a smaller number of large worms.

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7 Summary

The enchytraeids in five selected sites, of the Moor House National Nature Reserve, England, are shown to be important members of the moorland soil fauna, with maximum densities of nearly 300,000 per sq. m., representing a biomass of about 50 g. live weight in *Juncus squarrosus* moor. Specialized sampling methods were used to check on sampling and extraction bias and on population microstructure. The worms were found to be aggregated, having sampling distributions which were positively skewed and showed negative kurtosis. The vertical distribution was very superficial, most of the worms being concentrated in the top 2 cm. of the soil cores, especially in the $A_0L + F$ layers where present, and only driven deeper by cold or drying out. Downward movement was closely correlated with precipitation/evaporation ratios below unity. Although the hot dry summer of 1955 prior to this study was presumed to have decreased enchytraeid abundance in *Nardus* grassland, drought was not normally a recurrent threat to the worms especially in *Juncus* sites and densities increased through the late summer and autumn of 1956 and 1957 to peak numbers, correlated with wetter conditions.

7 Zusammenfassung

Es wird gezeigt, daß die Enchytraeiden von 5 ausgesuchten Standorten des Staatlichen Moor House Naturschutzgebietes ein wichtiger Bestandteil der Moorland-Bodenfauna sind. Sie erreichen im Juncus-squarrosus-Moor maximale Besatzdichten von annähernd 300000 Ex. per m², was einer Biomasse von etwa 50 g Lebendgewicht entspricht.

Spezialisierte Methoden wurden angewandt, um die systematischen Fehler der Probenentnahme und der Auslese, sowie die Mikrostruktur des Besatzes zu überprüfen.

Die Würmer wurden in nestartiger Verteilung gefunden; die Stichprobenverteilung ergab eine positive Schiefe und einen negativen Exzeß. Die Vertikalverteilung war sehr oberflächlich. Die meisten Würmer sind in den obersten 2 cm der Bodenausstiche konzentriert, besonders, wo vorhanden, in den $A_0L + F$-Horizonten und sie werden allein durch die Kälte oder durch Austrocknen tiefer getrieben. Abwärtsbewegungen waren mit dem Niederschlags-Verdunstungs-Verhältnis < 1 eng korreliert. Obwohl anzunehmen ist, daß der heiße Sommer des Jahres 1955, vor dieser Untersuchung, die Besatzdichte der Enchytraeen im Nardus-Grasland herabgemindert hat, war die Hitze normalerweise kein einschränkender Faktor für die Existenz der Würmer, besonders nicht an den Juncus-Standorten. Die Besatzdichte stieg vom Spätsommer und Herbst 1956 und 1957 auf Höchstwerte, die mit feuchteren Bedingungen korreliert waren.

8 References

BIRCH, L. C., 1957. The role of weather in determining the distribution and abundance of animals. Cold. Spr. Harb. Symp. quant. Biol. **22**, 203—218.

CHRISTENSEN, B., 1959. Asexual reproduction in the Enchytraeidae (Olig.). Nature **184**, 1159—1160.

CRAGG, J. B., 1961. Some aspects of the ecology of moorland animals. J. Ecol. **49**, 477—506.

DAVIDSON, J., & ANDREWARTHA, H. G., 1948a. Annual trends in a natural population of *Thrips imaginis* (Thysanoptera). J. Anim. Ecol. **17**, 193—199.

— — 1948b. The influence of rainfall, evaporation and atmospheric temperature on fluctuations in the size of a natural population of *Thrips imaginis* (Thysanoptera). J. Anim. Ecol. **17**, 200—222.

HUGHES, R. D., 1962. The study of aggregated populations. In: Progress in Soil Zoology (Ed. P. W. MURPHY) Butterworths, London 51—55.

IVLEVA, I. V., 1953. The influence of temperature and humidity on the distribution of Enchytraeidae (*Enchytraeus albidus* HENLE). Trudy Latvijskogo Otdelenija VNIRO **5**, 205—212 (in Russian).

JEGEN, C., 1920. Die Bedeutung der Enchytraeiden für die Humusbildung. Landw. Jahrb. Schweiz. **34**, 55—71.

NEYMAN, J., & SCOTT, E. L., 1957. On a mathematical theory of populations conceived as a conglomeration of clusters. Cold Spr. Harb. Symp. quant. Biol. **22**, 109—120.
NICHOLSON, A. J., 1957. The self-adjustment of populations to change. Cold Spr. Harb. Symp. quant. Biol. **22**, 153—173.
NIELSEN, C. O., 1952. Studies on Enchytraeidae 1. A technique for extracting Enchytraeidae from soil samples. Oikos **4**, 187—196.
— 1954. Studies on Enchytraeidae. 3. The micro-distribution of Enchytraeidae. Oikos **5**, 167—178.
— 1955a. Studies on Enchytraeidae. 2. Field studies. Natura Jutlandica **4**, 5—58.
— 1955b. Studies on Enchytraeidae. 5. Factors causing seasonal fluctuations in numbers. Oikos. **6**, 153—169.
NIELSEN, C. O., & CHRISTENSEN, B., 1959. Studies on Enchytraeidae 7. The Enchytraeidae. Critical revision and taxonomy of European species. Natura Jutlandica 8—**9**, 1—154.
O'CONNOR, F. B., 1955. Extraction of enchytraeid worms from a coniferous forest soil. Nature, Lond. **175**, 815—817.
— 1957. An ecological study of the enchytraeid worm population of a coniferous forest soil. Oikos **8**, 161—199.
PEACHEY, J. E., 1962. A comparison of two techniques for extracting Enchytraeidae from moorland soils. In: Progress in Soil Zoology (Ed. P. W. MURPHY) Butterworths, London 286—293.
REYNOLDSON, T. B., 1957. Population fluctuations in *Urceolaria mitra* (Peritricha) and *Enchytraeus albidus* (Oligochaeta) and their bearing on regulation. Cold Spr. Harb. Symp. quant. Biol. **22**, 313—327.
SALT, G., & HOLLICK, F. S. J., 1946. Studies of wireworm populations. 2. Spatial distribution. J. exp. Biol. **23**, 1—46.
SNEDECOR, G. W., 1956. Statistical Methods applied to experiments in agriculture and biology. 5th edition, Iowa State College Press, Iowa, pp. 1—534.
SVENDSEN, J. A., 1957. The distribution of Lumbricidae in an area of Pennine moorland (Moor House Nature Reserve). J. Anim. Ecol. **26**, 411—421.

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